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THE WINGS OF INSECTS.

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CHAPTER II.

The Venation of a Typical Insect Wing.

THERE are certain features of the venation of the wings of insects which occur in the more generalized forms of so large a proportion of the orders of this class that we are warranted in regarding them as typical of winged insects as a whole, and we are able to present a hypothetical type to which the wings of all orders may be referred.

This of course implies, what we believe to be the case, that all of the orders of winged insects have descended from a common winged ancestor. For it is not probable that had wings arisen more than once in this class that they should agree closely in their structural characteristics.

The recognition of the features of the wing venation that are common to the various orders of insects has been a matter of slow growth. Most writers on the subject have only attempted to work out the homologies of the principal veins within the limits of a single order; and thus have arisen the various systems of nomenclature of the wing-veins, which have done much to delay an appreciation of the uniformity of structure which really exists.

We will not take the space to trace out in detail the development of the idea that a uniform nomenclature of the wing-veins, based on homologies and, therefore, applicable to all orders, is possible. In 1870 Hagen attacked the problem in a paper, entitled "Ueber rationelle Benennung des Geäders in den Flügeln der Insekten."[1] But this essay apparently had little influence beyond calling attention to the importance of the subject. It was not till the appearance of the classic contribution of Redtenbacher[1] that any great progress was made. This paper, with its numerous illustrations drawn from nearly all orders of winged insects, is really the starting point in the actual solution of the problem.

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[1] *Stettiner Entomologische Zeitung*, Bd. xxxi, pp. 316-320.

Unfortunately, however, Redtenbacher was misled by the erroneous theory of alternating convex and concave veins elaborated by Adolph.[2] The result was that, although Redtenbacher recognized the homologies of the main stems of the principal veins, he, in his efforts to apply this theory, was led into many serious errors.

Then Spuler[3] followed, and, basing his conclusions on a study of the tracheæ that precede the wing-veins, worked out the type of the lepidopterous wings. Unfortunately, Spuler overlooked the trachea that precedes the first of the principal veins, and began his numbering with the second principal vein, which he designated as vein I.

The next step in advance was made by the senior writer of the present series of articles. In a text-book of entomology[4] he worked out the homologies of the wing-veins in the Lepidoptera, Diptera, and Hymenoptera. In the preface of that book he said:

> The principal features of the method of notation of wing-veins, proposed by Josef Redtenbacher, have been adopted. But as the writer's views regarding the structure of the wings of primitive insects are very different from those of Redtenbacher, the nomenclature proposed in this book is to a great extent original. The chief point of difference arises from the belief by the present writer that veins IV and VI do not exist in the Lepidoptera, Diptera, and Hymenoptera; and that, in those orders where they do exist, they are secondary developments.

But again, unfortunately, the work was not carried far enough. While the non-existence of the concave veins IV and VI of the Redtenbacher system was demonstrated for the orders named, no use was made of the wing venation in the other orders of insects; and his lack of definite knowledge on the subject made him willing to admit that these veins might exist as *secondary developments* in those orders with fan-like wings.

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[1] Josef Redtenbacher, Vergleichende Studien über das Flügelgeäder der Insecten. *Ann. des. k. k. naturhist. Hofmuseums*, Bd. i, 1886, pp. 153–232.

[2] G. Ernst Adolph, Ueber Insectenflügel, 1879.

[3] A Spuler, Zur Phylogenie und Ontogenie des Flügelgeäders der Schmetterlinge. *Zeit. f. wiss. Zool.*, Bd. liii, 1892, pp. 597–646.

[4] J. H. and A. B. Comstock, *A Manual for the Study of Insects*. Ithaca, N. Y., 1895.

At last the time has come when we believe that we understand the homologies of the wing-veins in so large a proportion of the orders of insects that we are able to present a hypothetical type to which the wings of all orders may be referred. And this type includes not only the principal veins, but also the chief branches of these veins.

It should be borne in mind that our main object at this time is merely to trace the homologies of the wing-veins, to the end that a uniform nomenclature for all orders can be adopted, and also to enable us to make intelligent use in taxonomic work of the characters presented by them. We do not presume to say that we have definitely determined the peculiarities of the venation of the wings of the stem form from which winged insects have descended. We feel, however, that we have reached a sufficiently near approximation to this desired end to warrant our conclusions regarding the homologies of the wing-veins, and to enable us to commend a nomenclature for them which we believe can be accepted as final.

In designating the wing-veins they may be either named or numbered. The simplest method is, doubtless, to number them; and had the system which was proposed by Redtenbacher been based on a correct understanding of the primitive type, nothing better could be desired. But it was not; and, as several modifications of the Redtenbacher system are already in use, it seems doubtful if uniformity in numbering them could be soon brought about.

From the great mass of names that had been proposed for the principal wing-veins, Redtenbacher selected a set of terms, to the acceptance of which no objection has been urged. It seems, therefore, that the surest way to bring about uniformity of nomenclature is to give up the attempt to apply a set of numbers to the wing-veins, and to use the names adopted by

Redtenbacher. These names and the abbreviations of them, which we shall use in our text as well as in the figures illustrating it, are as follows:

Costa, *C.*	Media, *M.*
Subcosta, *Sc.*	Cubitus, *Cu.*
Radius, *R.*	Anal veins, *A.*

In designating the branches of the forked veins we have adopted the principle of numbering them proposed by Redtenbacher and combine the numbers with the abbreviations of the names of the veins. Thus, the first branch of radius is designated as *radius-one;* and for this term the abbreviation R_1 is used.

In numbering the branches of the forked veins, *the same number is applied to homologous branches throughout the series of orders.* It is only in this way that the greatest use can be made of the characters presented by the wings in working out the phylogeny of groups.

But, in carrying out this plan, we have found that in certain orders, as, for example, the Neuroptera, there is a marked tendency towards the multiplication of the branches of some of the principal veins. It results from this that we find, in each of these orders, branches that have no true homologues in other orders, although in some cases analogous branches exist. As these supernumerary veins do not concern us while we are discussing the venation of the typical wing, we will postpone the consideration of them.

It frequently happens that the branches of a forked vein are reduced in number by the coalescing of two or more branches. In numbering such a compound branch the coalescence is indicated by the term applied to it. Thus, in very many insects, the second and third branches of radius coalesce throughout their entire extent, forming a single branch; this we designate as *radius-two-plus-three,* writing the term thus, R_{2+3}.

We will postpone for a time the discussion of the nomenclature of the cross-veins and of the cells of the wing, and proceed to a consideration of the hypothetical type to which we have referred.

There can be no doubt that the veins of the fore wings and of the hind wings are homodynamous. Any one that studies the subject much is impressed by this fact. A single diagram will be sufficient, therefore, to represent the venation of both pairs of wings of this type. Fig. 4 is such a diagram.

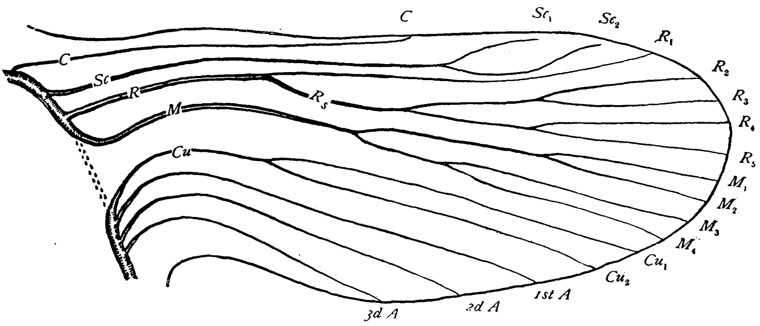

FIG. 4. — Hypothetical tracheation of a wing of the primitive nymph.

As the wing of a nymph is much more instructive than a wing of an adult for the purpose of determining homologies, we represent this ideal wing in that stage of development in which the forming veins appear as light-colored bands and the tracheæ as dark lines. This stage in the wings of an actual nymph is well shown by the half-tone reproductions of photographs of the wings of a nymph of Nemoura, given in Chapter I (Figs. 2, 3).[1] In our hypothetical type we have represented only the tracheæ, which precede the forming veins.

By representing the wing of a nymph we are able to represent the basal connections of the tracheæ that precede the veins, and thus show which are principal veins and which are branches of them. This point has received very careful attention, a large number of nymphs and pupæ, representing nearly all of the orders of insects, having been examined especially for this purpose. Fortunately, this evidence confirms the conclusions reached by various writers who have studied only the wing-veins of the adult, and merely serves to remove any doubt there might have been regarding these conclusions.

Another point which can be brought out in this way is the

[1] *American Naturalist*, January, 1898, vol. xxxii, pp. 46, 47.

distinction between principal veins and cross-veins. For, although in certain highly specialized wings, as, for example, those of the Odonata, every cross-vein is preceded by a trachea, we have found that, as a rule, the secondarily developed cross-veins are not preceded by tracheæ. The figures of Nemoura in Chapter I illustrate this.

In the adult the front, or costal margin, of the wing is usually strengthened by a vein or a vein-like structure; this is designated as the *costa*. A study of immature wings shows that, although the costa usually extends more or less nearly to the apex of the wing, the costal trachea is, as a rule, greatly reduced. This reduction of the costal trachea has led to its being overlooked by previous writers, and to a denial of its existence by Brauer and Redtenbacher.[1] It is true that Brongniart figures what he believed to be the costal trachea in the nymph of a dragon fly;[2] but the structure which he represents is evidently the edge of the wing within the wing sheath of the nymph.

We have succeeded in finding the costal trachea in nearly all of the orders of winged insects, and have found that in widely separated forms, as in many Hemiptera and in the more generalized Hymenoptera, it extends nearly or quite to the apex of the wing. Further details regarding it will be given in the treatment of the separate orders. It is only necessary to state here that we have abundant evidence to support the view that the costa of the primitive insect wing resembled the other wing-veins in being preceded by a trachea, and that the origin and course of this trachea was probably very nearly as represented by *C* in Fig. 4. In the photographs of the wings of a nymph of Nemoura, reproduced in Chapter I, the costal trachea is not evident; but figures will be given of other Plecoptera in which this trachea is as distinct as any and extends to the middle of the wing.

The second of the principal veins of the wing is designated as the *subcosta*. This extends more or less nearly parallel with the costa and but a short distance from it. In those orders where there are many wing-veins it gives off numerous small branches to the costa; in the orders where there are few wing-veins it appears in the adult to be an unbranched vein. But a study of the subcostal trachea in nymphs and in pupæ shows that it is forked in at least several widely separated orders; we have, therefore, represented it so in our type (Fig. 4, Sc_1 and Sc_2). In adult wings the branches of the subcosta are usually either wanting or appear as cross-veins. In those orders in which the wing is corrugated the subcosta lies at the bottom of a furrow, which stiffens the costal edge of the wing.

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[1] *Zool. Anz.*, Bd. xi, 1888, pp. 443–447.

[2] *Rech. sur les Insectes Fossiles*, Pl. viii, Fig. 1, *a*.

The third vein is the *radius*. This is the most prominent vein in the wing; and it is the one which, from the great variety of its modifications, offers more often than any other vein obvious characters of use in taxonomic work. In spite of the wide differences of form of this vein in the different orders, it is now clear to us that these various forms have all been derived from a type which still exists, but slightly modified, in the more generalized Trichoptera, Mecaptera, Diptera, and Lepidoptera, and in certain genera of several other orders. In its typical form this vein is five-branched (Fig. 4, R_1–R_5). The main stem of the vein separates into two divisions; the first of these is simple and is more or less nearly a direct continuation of the main stem — this is *radius-one* (R_1); the second of the principal divisions of radius is typically four-branched, and on account of the frequency of the necessity of making reference to it a special name has been applied to it, the *radial sector* (R_s). The radial sector separates into two divisions (R_{2+3} and R_{4+5}); and each of these again separates into two divisions, the former into *radius-two* (R_2) and *radius-three* (R_3), and the latter into *radius-four* (R_4) and *radius-five* (R_5).

The vein occupying the center of the wing is the *media* (M). In those orders in which it retains most nearly its primitive form it is usually three-branched; but the fact that in the more generalized members of several widely separated orders it is four-branched leads us to believe that it was four-branched in the stem form of winged insects. The branches are designated as *media-one* (M_1), *media-two* (M_2), *media-three* (M_3) and *media-four* (M_4), respectively.

The fifth principal vein is the *cubitus* (*Cu*); this vein separates into two branches, — *cubitus-one* (Cu_1) and *cubitus-two* (Cu_2).

Between the cubitus and the anal margin of the wing there are typically three veins; these are commonly termed the anal veins. We will distinguish them as the *first anal* (*1stA*), the *second anal* (*2dA*), and the *third anal* (*3dA*), respectively, the first anal being the one nearest to the cubitus.

The first anal vein is generally simple; but in those orders where the anal area of the wing is expanded the second and third anal veins become separated into many branches, which form the supports of the fan-like portion of the wing.

Before leaving the discussion of this hypothetical type it seems necessary to say a little regarding the basal connections of the tracheæ that precede the wing-veins. In what appears to us to be the most generalized type, the tracheæ that supply the wing with air arise from two distinct trunks, as shown in Fig. 4. The first of these trunks is a branch of the dorsal longitudinal trachea of the thorax; the second, of the ventral longitudinal trachea. This type exists in all Plecoptera that we have examined and in certain cockroaches; we have not found it elsewhere.

The two groups of wing-tracheæ thus formed may be designated as the *costo-radial group* and the *cubito-anal group*, respectively. When the two groups are distinct, the trachea that precedes the media is a member of the the costo-radial group.

In most insects there has been developed a transverse trachea connecting these two groups of tracheæ; the position of this *transverse basal trachea* of the wing is indicated in the figure by dotted lines. Frequently the transverse basal trachea is indistinguishable from the two main trunks which it connects, the three forming a single, continuous, transverse trachea, from which arise all of the wing tracheæ. All of the stages of this development have been found by us within the Orthoptera.

When a transverse basal trachea is formed, the medial trachea (*i.e.*, the trachea that precedes media) tends to migrate along it towards the cubito-anal group of tracheæ, and often becomes united with that group. This is well shown in certain Orthoptera and in the Hemiptera. In some cases the base of the radial trachea tends to follow the base of the medial in its migration along the transverse basal trachea towards the cubito-anal group (Acrididæ).

We have found no indication that the formation of a transverse basal trachea and the subsequent migration along it of the base of the medial trachea is influenced at all by the flight function of the wing, as the arrangement of the wing-veins does not appear to be modified by it. It should be remembered that the transverse basal trachea and the bases of the wing tracheæ are within the thorax of the adult insect, and are thus beyond the influence of the migrations of the wing-veins.

It is probable that these changes have to do with improving the air supply of the wing; but we have not sufficient data, as yet, to warrant a definite statement on this point. The important thing for the purposes of the present discussion is that one must know of this tendency on the part of the medial trachea to migrate along the transverse basal trachea in order to be able to recognize it in its various positions.

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